

¹ Simulated Mima mounds emerge from small interactions

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⁴ **Abstract**

The Mima-mound-and-vernal-pool topography of California is rich in endemic plant and invertebrate species, but we do not know how this unusual environment is created or maintained. Burrowing rodents have been observed to move soil upwards at annual rates sufficient to maintain the mounds despite erosion, but there is no tested explanation of this behavior. We propose that the mounds are an emergent effect of small-scale (10 cm, 1 day) interactions between topography, hydrology, plant growth, and rodent burrowing. A cellular automata simulation of these processes both generates and maintains mound-pool topography with minimal dependence on initial conditions, and can also describe mound morphogenesis on slopes, where observed mound geometry is distinct from that on level ground.

¹⁴ **Introduction**

Mound-pool topography, or Mima mounds, were common on many landforms in California, Oregon, and Washington before 1850 [Smith and Verrill, 1998]. The numerous small vernal pools of this topography are habitat for endemic species of plants and animals [Bradford, 1992, Skinner and Pavlik, 1994]. Better understanding of natural mound-pool maintenance should improve the protection and reconstruction of habitat [Zedler, 2009].

20 Mound-pool topography formation and maintenance has been ascribed to earthquakes, erosion
21 and deposition by wind or water, relict tree-stumps, or glacier thaw, but these hypotheses do not
22 fit all the similar mound fields [Washburn, 1988]. The fossorial hypothesis, that burrowing rodents
23 are responsible [Turner, 1896], has been gaining strength with detailed observations, usually of
24 pocket gopher activity [Cox, 1990, Horwath and Johnson, 2006, Reed and Amundson, 2007].
25 (Many studies of fossorial rodents refer to the loose material removed from their burrows every
26 few days as ‘mounds’; these piles are from 10 cm to a meter across, and are unconsolidated,
27 unvegetated sediment. This paper refers to these piles as ‘tailings’, and only to the vegetated,
28 Mima-type mounds, diameters 1 m to 10 m, with developed pedogenic features, as ‘mounds’.)
29 It is still unclear what causes gophers to maintain mounds in some regions but not in others.
30 Centering mounds on the nests or favored foods of gophers [Dalquest and Scheffer, 1942, Horwath
31 and Johnson, 2006] does not explain why mounds only occur in some of the prairies inhabited
32 by *Thomomys* and *Geomys* species. Assuming that mounds exist only where intermound soil is
33 too thin to contain burrows is contrary to observations of fossorial activity in intermound regions
34 during dry periods (pers. obs., Jepson Prairie, Nov. 2011). In many California grasslands fossorial
35 rodents increase erosion and reduce variation in soil thickness [Yoo et al., 2005], particularly on
36 shallow slopes [Reichman and Seabloom, 2002], which would tend to erase mounds rather than
37 maintaining them. Moreover, not only is there no evidence that rodents in mound-pool regions
38 have developed mound-building instincts, there is some evidence against it: Patton and Smith
39 [1990] classifies *Thomomys bottae* of the whole North Central Valley from the Delta to Oregon
40 as one genetic group, with no significant genetic heterogeneity between the two populations in
41 the group. This region includes great swathes of surviving and pre-colonization vernal pool and
42 mound-pool habitat and also non-pool habitat [Holland, 1998]. Pocket gophers in flood-irrigated
43 alfalfa fields live in the raised field edges [Pipas et al., 2000], suggesting that the gopher mound-
44 building response is not an immediate reaction to inundation.

45 I hypothesize that surface irregularity and annually-increasing inundation are enough to both
46 localize and direct fossorial activity in a way that amplifies the surface irregularity into mound-

47 depression microtopography without any mound-specific instinct or initial condition. Specifically,
48 plant species and growth is organized in space by irregular soil surface, and in time by seasonal
49 inundation [Lazar, 2004, Zedler, 1987]. Fossorial rodents forage on the organized plants. For
50 instance, pocket gophers, a fossorial rodent common to California, have food preferences [Hunger-
51 ford, 1976, Tilman, 1983], possibly including phenological preferences[Behrend and Tester, 1988].
52 Pocket gophers reach population density high enough to disturb each point in a natural grassland
53 every 3 to 5 years[Hobbs and Mooney, 1995] and can individually move 8 to 66 liters of soil a
54 day [Andersen, 1987]. I hypothesize that rodent attraction to plants at the water margin biases
55 rodent movement downward and therefore biases soil movement upward. For fossorial activity
56 to maintain mounds against erosion, the net upward movement of soil must be great enough to
57 counterbalance the rapid erosion of rodent tailings as well as the general erosion rate.

58 This model explains why the Mima mounds are associated with seasonally-inundated land-
59 scapes [Nikiforoff, 1941, Smith and Verrill, 1998] more parsimoniously than do explanations de-
60 pending on either universal or adaptive behavior [Dalquest and Scheffer, 1942, Mielke, 1977, Cox
61 and Allen, 1987]. Behavior common to an entire rodent species, such as nest-building, should tend
62 to create mounds in all landscapes if it does in any landscape. An emergent process of mound
63 creation is also testable, and consistent with claims of recent mound re-formation [Johnson, 2011].

64 The main processes that interact in a mound-pool landscape were described independently
65 and combined in a cellular automata (CA) model of landscape development. In a CA, physical
66 space is represented by discrete cells. Each cell stores the values of one or more state variables,
67 so that each state variable is represented discontinuously over the whole space. The laws of the
68 simulated system are formulated in terms of the state variables in each cell and a specified set
69 of its neighbors. Each law may require that any set of the state variables in the current cell and
70 its neighbors be updated based on their joint states. Time is simulated by updating all the cells,
71 checking that conserved values are in fact conserved.

72 CA have two particular strengths. First, the representation of processes at local scales is often

⁷³ a good match for the measurements we can make to test the models. Second, CA can demonstrate
⁷⁴ features that develop not ‘top-down’, from central or controlling agents, but as emergent processes
⁷⁵ requiring the interactions of all the constituent parts. Many landscape and ecology problems that
⁷⁶ have resisted top-down explanations are tractable to CA and other emergent methods [Fonstad,
⁷⁷ 2006].

⁷⁸ Methods

⁷⁹ Model representation

⁸⁰ In this model, the simulated landscape is broken into square cells representing an area 10
⁸¹ cm on a side. 10 cm is approximately the size of a large *Thomomys* burrow or a small surface
⁸² tailings mound of burrow ejecta. Each cell stores four state variables (Table 1). Four processes
⁸³ were identified that occur in each simulated day: plant growth, rodent activity, soil erosion, and
⁸⁴ inundation or evaporation. Processes operate on the state variables and interact only through the
⁸⁵ state variables.

⁸⁶ Each process is described with several alternate algorithms representing competing common
⁸⁷ descriptions of the real-world process (Table 2). A complete simulation of a landscape requires that
⁸⁸ the initial topography be specified and each of the four processes be assigned one specific algorithm
⁸⁹ of the several available. The simulation then goes forward by running each of the sub-processes
⁹⁰ in turn for each simulated day. This system allows simulated comparison and manipulation ex-
⁹¹ periments; one simulation may be copied, and one state variable array or sub-process in the copy
⁹² changed to an alternative. The pair of simulations are run in parallel, and the results compared.

⁹³ The model is written in Python, using *numpy.random* where stochastic behavior needs to be
⁹⁴ simulated and *PIL.Image* and *scipy.ndimage* for image analysis [Jones et al., 2001–].

95 **Parametrization**

96 The model is parameterized with measurements made at Jepson Prairie Nature Reserve, a
97 well-studied, pedologically young [Smith and Verrill, 1998] basin-rim formation in the Central
98 Valley of California. Jepson Prairie includes mound-pool formations in the Antioch-San Ysidro
99 Complex. Where these measurements cannot be made, we use values from the literature for the
100 Central Valley. Sensitivity testing is done by comparing output simulated with parameter values
101 at the mean and extrema of given ranges.

102 Where measurements are not available, the model uses values or algorithms that are pessimal
103 for the generation of microtopographic structure. For instance, the initial topography of a site
104 could be perfectly flat or randomly irregular on the 10 cm scale. The introduced simulated rodents
105 were generally added at the center of the model, not randomly across the landscape. These were
106 chosen to make mound-pool initiation less likely than in the real-world cases: for instance, a real
107 California grassland before the development of a restrictive claypan or hardpan might have had
108 grass tussocks or shrubs at meter or ten-meter average spacing, with a slight elevation and improved
109 drainage at the base. Real pocket gophers have spatially distinct, nest-centered territories [Lacey,
110 2000].

111 **Acceptance tests**

112 There is aerial photography of a section of the Greater Jepson Prairie during the inundated
113 period available as a real-world example of the degree and kind of organization reported in the
114 real world as Mima mounds (Fig. 1). Keeley and Zedler [1998] characterize mound-pool microto-
115 pography as being rain-filled and evapotranspiration-emptied, not connected to overland drainage
116 systems. This distinguishes them from vernal swales and most other temporary wetlands. In the
117 model, we distinguish ‘pool’ from ‘nonpool’ landscapes by checking for this disconnection. An im-
118 age of the landscape is generated at the most inundated season of the year, and we count distinct
119 underwater regions. This can be done automatically with *ndimage.watershed_ift*. A landscape

120 averaging at least 0.05 pools/m^2 is counted as a ‘pool’ landscape. Most simulations using the final
121 model have a higher density of pools than that (Fig. 2).

122 Similarly, a ‘mound’ landscape has at least 0.05 mounds/m^2 , where a mound is a distinct
123 region in the highest 20% of the distribution of elevations. This distinguishes a mound-pool
124 landscape from a landscape with pools that seem to be pockmarked into a level or branching
125 surface.

126 Results

127 In computer simulations, these small interactions are enough to turn a randomly irregular
128 surface into moundlike microtopography without any additional organizing principle (Fig. 2).
129 Identifiable mound-pool structures develop from random or flat topography in approximately 250
130 simulated years, where observation estimates mound re-formation at 50 or 80 years [Johnson,
131 2011].

132 The minimal full set of tested interactions that generates mound-pool topography, within five
133 hundred simulated years, is:

- 134 ○ Plants grow fastest when neither waterlimited nor underwater.
- 135 ○ Fossorial rodents move towards the densest adjacent plant growth and consume some of it,
136 as in Reichman and Smith [1985].
- 137 ○ Rodents don’t tunnel underwater.
- 138 ○ Rodents will only occupy a cell next to another rodent to avoid drowning.
- 139 ○ Rodents move a volume of earth behind them as they travel; maximum volume estimated
140 from Andersen and MacMahon [1981].
- 141 ○ Soil is eroded at intervals during the rainy season. Unvegetated soil erodes more quickly
142 than vegetated soil.

- 143 ○ The soil is periodically over-saturated. This could represent flooding in a drainage basin or
144 seasonal rain in a region with impermeable soil layers.
- 145 ○ The highest water level increases over the first two hundred years.

146 The result of these processes is a four-stage feedback loop:

- 147 ○ Irregular topography directs water into depressions
- 148 ○ Plants grow most richly at the edge of the water
- 149 ○ In the wet season, rodents live upslope but move downslope to forage
- 150 ○ Rodents push earth uphill when they move downhill, reinforcing the irregular topography.

151 The alternate algorithms for each of these that do not produce mound-pool topography, from
152 level, random, or sloped initial topography, are marked in Table 2 with ‘*Fails*’.

153 There are two parameters to which the system is particularly sensitive. The rodents’ mutual
154 avoidance radius may be 0, 1, 2, or 3 cells wide. Mound-generation improves (from 2/3 success on
155 random initial topography, to success on all initial topography) when the radius is greater than
156 0 cells wide. Mound generation may occur more quickly with greater radii, but success does not
157 change. The full model uses a 1-cell radius, as the least restrictive.

158 The difference in erosion rates between vegetated and unvegetated soil is also significant. The
159 full model assumes that vegetated soil erodes 0.2 times as quickly as unvegetated soil, an estimate
160 derived from preliminary observations at Jepson Prairie. If vegetated soil erodes 0.8 times as
161 quickly as unvegetated soil, the landscape develops neither mounds nor pools, as colluvium from
162 the high regions fills the potential pools (Fig. 3).

163 **Alignment on slopes**

164 One addition to the full model above was a rough test of the system on a slope, adding
165 overland flow and advection of sediment. Terrace landforms on the eastern edge of the Central

166 Valley have well-developed, densely packed Mima mounds (Fig. 4). The mounds extend into the
167 gullies and channels at the edge of the terraces, and on those slopes the mounds are aligned and
168 often extended along the line of fall. In a very rough simulation of overland flow (Fig. 5), an
169 initial condition of smooth, divided mounds, aligned or offset, erode into alignment along the fall-
170 line. Rodent activity fills in the space between upslope and downslope mounds, creating extended
171 mounds in the observed direction.

172 Discussion

173 Emergent mound-pool development, even in simulation, makes the fossorial rodent hypothesis
174 stronger because it explains the co-occurrence of mound-pool systems over restrictive layers or in
175 floodplains without requiring adaptive rodent behavior or initial topographic conditions that we
176 cannot observe or test. The small-scale interactions it depends on can be observed in the field and
177 adjusted for parametrization or spatial correlation, or ruled out.

178 The mound-pool organization occurs because the full model is a reaction-diffusion system,
179 qualitatively like the Belousov-Zhabotinsky reaction, which generates mazes or dots of chemical
180 states depending on ratios of reaction rates. It is easy to get patterns from a reaction-diffusion
181 system [Cantrell and Cosner, 2003], so this is a valuable explanation only insofar as the processes
182 match ecosystem processes observed in the field.

183 Further research, therefore, will concentrate on fieldwork to examine the spatial relations
184 between the processes in the full model, and in modeling more complex processes that may be
185 significant over geological time. For instance, the current model ignores rodent nest and territory
186 maintenance. Since these rodents maintain nests and territories in all their habitats, nests are not
187 a sufficient explanatory feature. However, territory geometry might make the mound shapes and
188 sizes more realistic. Rodent attraction to the edge of surface water could be based on a preference
189 for soil of a particular saturation, as in [Andersen and MacMahon, 1981].

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192 fossorial hypothesis, and to John Harte for discussions of ecosystem modeling.

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Table 1: State variables maintained by each cell of the CA

Elevation	Soil surface, from upper limit of the developing restrictive layer.
Vegetation density	A general measure of green plant density, from 0 to 1.
Rodent presence	Whether a fossorial rodent is currently in the cell.
Water table	Depth of the water table above the restrictive layer; in a level soil, this is the same for every cell.

Table 2: Available processes for each of the four main landscape processes modeled

Hydrology	Well-drained soil, in which no perched water develops and all cells are equally saturated during the rainy season. <i>Fails</i>
	Restricted-drainage soil, in which the perched water table rises during the rainy season and evaporates away in the dry season.
	Overland flow, in which cells below the water table periodically move in a fixed direction, potentially picking up or depositing loose sediment.
Plant growth	Plants grow faster when closer to the water level, in a linear relation.
	Plants grow equally well everywhere, during the rainy season. <i>Fails</i>
Erosion	Soil moves between Von Neumann-neighbor cells, proportionally to the lack of vegetation and the elevation difference. Fast, and develops mound-pool landscapes when Moore-neighborhood erosion does, but the results show the alignment of the grid (see Fig. 3).
	Soil moves between Moore-neighbor cells, proportionally to the lack of vegetation and the elevation difference.
Rodent activity	Rodents will not move or stay below the water table, and cannot occupy a cell already occupied by another rodent. They will move to the adjoining cell with the greatest vegetation; if neighboring cells are tied, they choose randomly. <i>Fails</i>
	As above, but rodents will not move into a cell adjacent to another rodent.
	Rodents will not move or stay below the water table, and cannot occupy a cell already occupied by another rodent. Among acceptable cells, they change direction with a probability proportional to the richness of the vegetation in their current cell. <i>Fails</i>

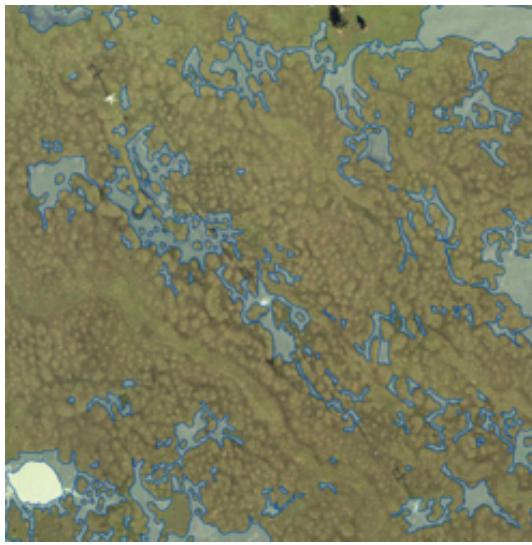


Figure 1: Aerial photo of a quarter section (0.79 m^2) of Burke Ranch, CA, in the wet season. Vernal pools are digitally outlined. Photo from Westervelt Ecological Services.

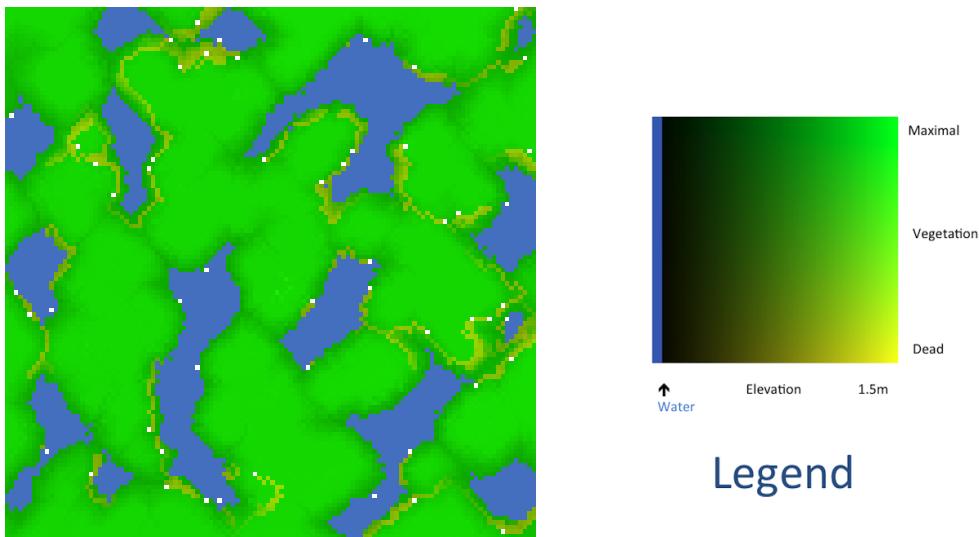


Figure 2: Results of the full model in 300 simulated years from the beginning of surface inundation. Shown at the highest water level of the year. 12 m a side.

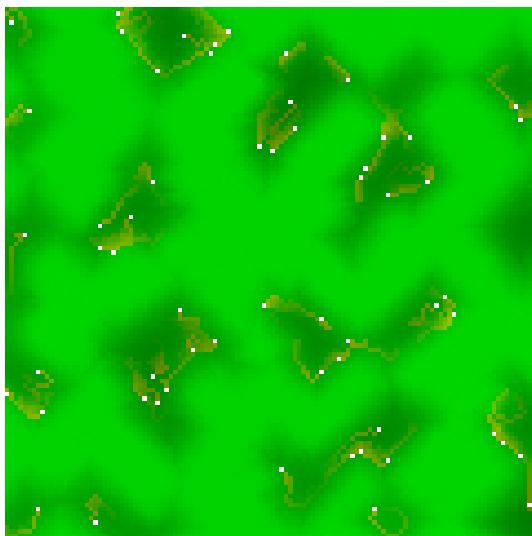


Figure 3: Full model *except* that vegetated soil erosivity is 0.8 that of gopher-excavated tailings; in full model, 0.2. Simulation 450 years from a random initial surface and the initiation of perched water.

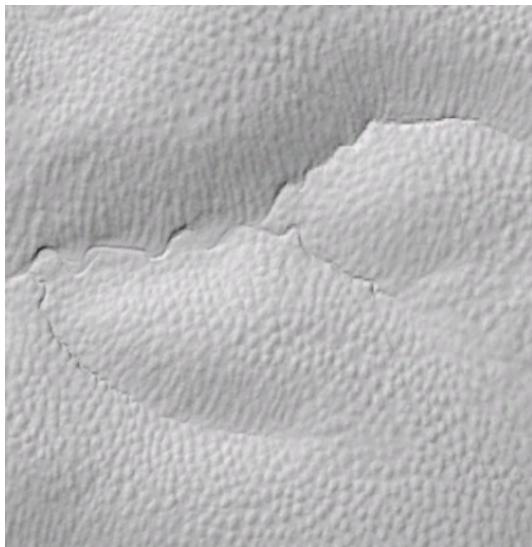


Figure 4: NCALM LiDAR of Mima mounds near Merced, California. Lat 37.433684° , lon - 120.418560° . Available from http://calm.geo.berkeley.edu/zip/merced_ug727_4145.zip, and as a Google Earth overlay.

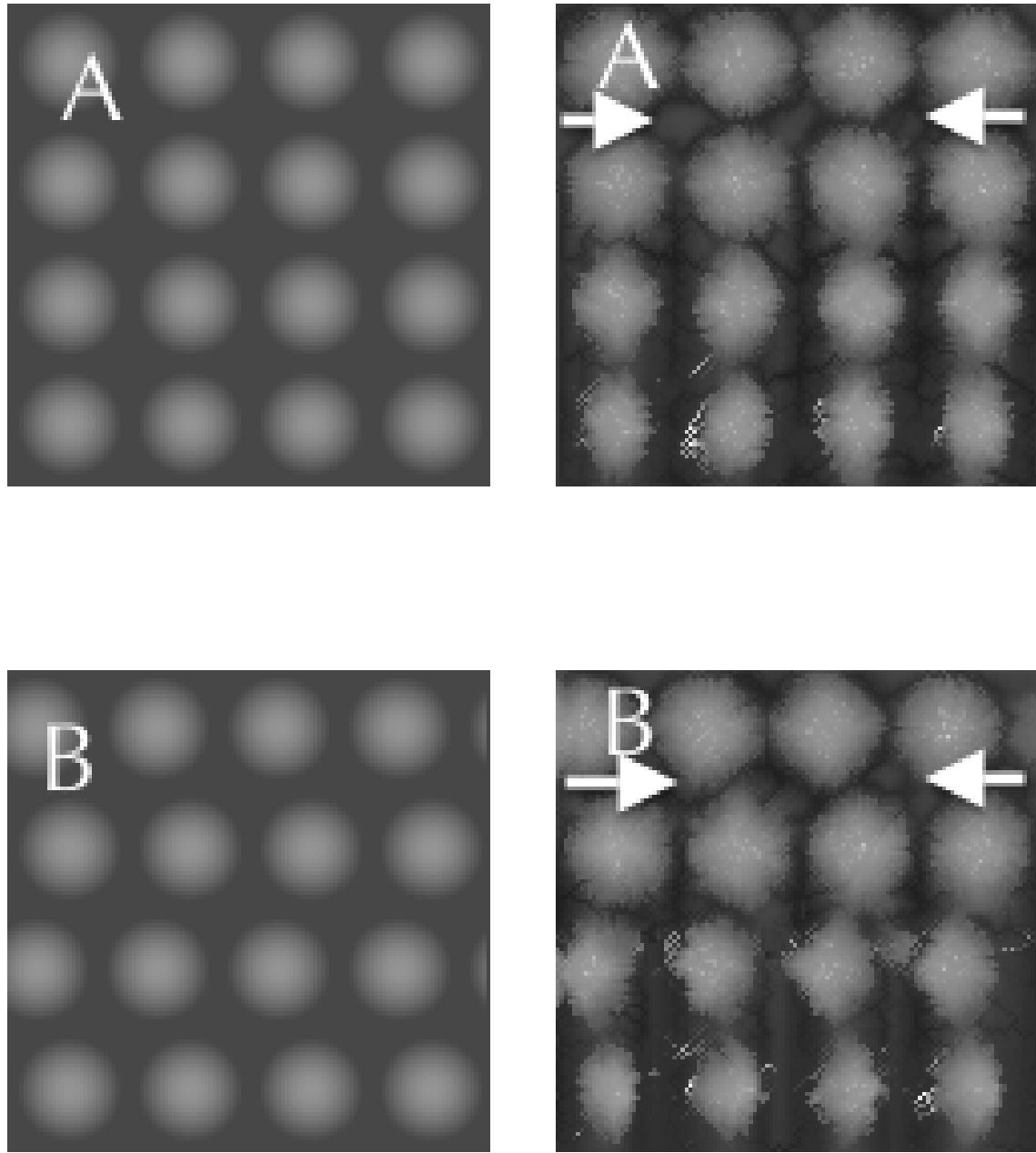


Figure 5: Elevation plot (light color is elevated) of mounds on a slight slope; aligned (A) or not (B). Slope begins between the first and second row of mounds (between arrows) and moves toward the bottom of the image. Overland flow moves unvegetated sediment. Erosion is increased below intermound gaps, forcing alignment downslope. Rodent activity moves soil into the protected region below mounds, generating mound extension. Highly stylized hydrology. 12 m a side, simulated 150 years.